A REVIEW OF THE MESOZOIC OSTRACOD GENUS *PROGONOCYTHERE* AND ITS CLOSE ALLIES

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ABSTRACT. The cytheracean ostracod genus *Progonocythere* and its immediate allies in the Jurassic and Cretaceous are reviewed. All known species of 12 genera are considered. Only five of these genera (*Dromacythere, Fastigatocythere, Glyptocythere, Majungaella, Progonocythere*) remain valid; the seven rejected genera are *Amicytheridea, Glyptogatocythere, Malzia, Novocythere, Strictocythere, Tickalaracythere* and *Zerqacythere*. We consider that the level of validity among other cytheracean groups is probably similar and that this reflects a serious decline in taxonomic standards based upon the inability of many authors to discriminate between generic and specific characters. The simple philosophy that differences of kind are generic, while those of degree are specific, seems to be largely ignored by many present day ostracod workers. We advocate that, wherever possible, the diagnoses of existing genera be expanded to embrace end-members, rather than the continual creation of so many superfluous generic taxa based on specific characters, which will eventually render the science inoperable.

UNFORTUNATELY, a very large number of ostracod genera erected in the past 25 years or so have been discriminated on the basis of what the present authors consider to be specific characters. The senior author, in preparing various families of the Cytheracea for the revision of the *Treatise on invertebrate palaeontology*, *Part Q*, *Ostracoda* of which he is coordinating author, has been struck by the very large number of monotypic, or near monotypic, genera erected on extremely flimsy evidence. Any species with the slightest morphological divergence from the norm of a genus is immediately denominated as new, notwithstanding that it may be the sole representative of that taxon. The more logical procedure, of regarding such newly discovered species as new morphological end members of an existing plexus of species is rarely adopted. Some of the prolific creators of such spurious taxa are possibly of the opinion that the original diagnosis of a genus is sacrosanct and immutable when, in fact, it must inevitably be expanded as new species are encountered. In the production of the *Treatise* revision, a large number of new, ornate podocopid genera of various families have been subsumed as junior synonyms within pre-existing genera.

It is almost always taxa with prominent ornamentation which are associated with this form of generic 'splitting'. Smooth ostracods, always difficult to deal with taxonomically, are much more stable generically. In many cases, it seems that authors do not understand the differences between what are primary and secondary aspects of ostracod ornament. For example, if ten or so species of a genus all have the same primary ornament, (say) of three parallel ribs, then to encounter a species similar in all other respects but with only two ribs or with four, is possibly to have found something worthy of separate generic status. However, if all of those ten species are, in their intercostal areas, differently ornamented (this being a secondary feature), these differences are important specific characters and no more. All too often, authors have used such secondary ornamentation to create new genera and complicate, almost beyond function, the existing taxonomic system. One needs only to look at the near total anarchy which exists in the Foraminiferida, with hundreds of monotypic genera, to know that this is a practice which should be suppressed.

To work in taxonomy is to exercise judgement and not to try to break records. If authors were to apply the philosophy that differences of kind were generic, while those of degree were specific, then a much more rational system would prevail.

In the following study, we examine 12 Mesozoic podocopinid cytheracean ostracod genera of the family Progonocytheridae Sylvester-Bradley, most closely related in their morphology to the genus *Progonocythere* Sylvester-Bradley (Table 1). We find that seven are readily referable to other genera

Stratigraphical and geographical distribution. New distributions resulting from this review in bold Genus Author and date Type species Progonocythere Sylvester-Bradley, 1948 P. stilla Bajocian-Oxfordian: Britain, Europe, Israel, Egypt, Saudi Arabia, India, Madagascar; L. Bajocian: Australia Glyptocythere Brand and Malz, 1962 G. tuberodentina Bajocian-Bathonian: Britain, Europe Grekoff, 1963 Majungaella M. perforata Callovian-Maastrichtian: East and South Africa, Madagascar, India, Australia, S. Chile, Argentina, Falkland Plateau, E. Brazil Malzia Bate, 1965 M. bicarinata Bajocian: Britain Fastigatocythere Wienholz, 1967 Bathonian-Kimmeridgian: F. rugosa Britain, Europe, Egypt, Jordan, Saudi Arabia, East and South Africa, Madagascar, India; Lower Bajocian: Australia Novocythere Rossi de García, 1972 N. santacruziana Aptian-Albian: Argentina Amicytheridea Bate, 1975 Procytheridea ihopyensis Bajocian-Callovian: Saudi Arabia, East Africa Campanian-Maastrichtian: east Tickalaracythere Krömmelbein, 1975 T. ticka Brazil; Albian–Campanian: Australia G. malzi Bathonian: Jordan; Glyptogatocythere Basha, 1980 Bajocian-Bathonian: Egypt Z. subiehiensis Bathonian: Jordan, Egypt, Saudi Zerqacythere Basha, 1980 Arabia Ware and Whatley, 1980 D. sagittata Upper Bathonian: Britain Dromacythere Strictocythere Sheppard in Brand, 1990 Progonocythere polonica Upper Bathonian: Britain, Europe; Lower Bajocian: Australia

TABLE 1. The twelve genera of Progonocytheridae considered here, arranged in date order, with type species and geographical distribution. The five genera considered to be valid are in italics.

within the complex and that only five are valid. This, of course, is a matter of judgement. However, we have in the course of this study, examined and considered all of the species attributed to each of the original 12 genera. Sad to relate, in many areas of the *Treatise* revision, approximately the same percentage of validity seems to obtain!

THE GENERA

In the *Treatise* revision, the Progonocytheridae will comprise only genera with entomodont/lobodont hinges (*sensu* Moore and Pitrat 1961; *non* Van Morkhoven 1962). The family will be divided into the Progonocytherinae, comprising subovate to subtriangular genera with a convex

dorsal margin and more or less strong ventro-lateral tumidity, similar to those discussed here, and another subfamily which will embrace subrectangular to subquadrate genera. The latter group comprises such genera as *Acanthocythere* Sylvester-Bradley, 1956, *Afrocytheridea* Bate, 1975, *Lophocythere* Sylvester-Bradley, 1948, *Neurocythere* Whatley, 1970, *Terquemula* Blaszyk and Malz, 1965, and *Trichordis* Grekoff, 1963. These are the subject of a subsequent review by the authors which is in preparation.

In order to facilitate comparison between them, the most important morphological characters of the 12 genera included in the present study, are outlined in Table 2; those which we consider to be valid are in italics.

Progonocythere Sylvester Bradley, 1948

This genus was based initially on three species: *Cythere blakeana* Jones, 1884, *C. juglandica* Jones, 1884 and *Progonocythere stilla*, the last named being a new species chosen by Sylvester-Bradley as the type. All these species had the 'hinge characteristics of the subfamily': a straight hinge composed of three elements, anterior, posterior and median, in which the median element is further subdivided into antero-median and postero-median parts. In the larger (left) valve, the anterior and posterior elements are short, loculate sockets; the median element is a bar, the anterior portion of which is always dentate, the posterior portion being denticulate. In the smaller (right) valve, the anterior and posterior elements are short dentate bars, the anterior always, the posterior usually, denticulate. The median element is clearly divided into an expanded anterior groove with four or five distinct loculi, and a posterior groove narrower than the anterior, with more numerous but less clearly defined locellae. The above description of the entomodont hinge is modified from Sylvester-Bradley (1948, p. 189).

Whatley (1964) reviewed the status of the genus and indicated that some species added since 1948 were better accommodated elsewhere. Forms with antimerodont rather than entomodont hinges in particular were excluded. Some of the species rejected from the genus by Whatley (1964) have subsequently been described as new genera, e.g. *Progonocythere hieroglyphica* Swain and Peterson is now assigned to *Pseudoperissocytheridea* Mandelstam (see Whatley 1970, p. 351).

In the present review, we have encountered numerous species placed in *Progonocythere*, mostly since 1964, which we consider would be best removed from the genus and accommodated elsewhere. These are listed below (in date order of first citation of combination) together with two of Sylvester-Bradley's (1948) original three species which have been transferred since 1964.

1. *Progonocythere juglandica* (Jones, 1884) *in* Sylvester-Bradley 1948 (pl. 12, figs 5–6), from the Middle Jurassic of Europe and Madagascar was assigned to *Fastigatocythere* by Wienholz (1967).

2. *Progonocythere blakeana* (Jones, 1884) *in* Sylvester-Bradley 1948 (pl. 12, figs 3–4), from the Middle Jurassic of Europe, is assigned to *Terquemula* Blaszyk and Malz following Bate (1969, p. 393) who designated, discussed and illustrated the lectotype.

3. *Progonocythere caswellensis* Brown, 1957 (*in* Catalogue of Ostracoda 1952, figs 14–15), from the Upper Cretaceous of North Carolina, should be included in *Pseudoperissocytheridea* Mandelstam because of its antimerodont hinge and ornament.

4. *Progonocythere? bemelenensis* (Veen) and *Progonocythere subcarinata* (Bosquet) *in* Howe and Laurencich 1958, p. 470, from the Maastrichtian of South Limburg, Holland, are both *Brachycythere* Alexander.

5. *Progonocythere* sp. A Wall, 1960 (pl. 28, figs 12–14), from the Callovian of Saskatchewan, Canada, resembles *Glyptocythere* Brand and Malz, but its hinge is antimerodont and it should be removed from the Progonocytheridae.

6. *Progonocythere juglandica* (Jones) subsp. *malgachica* Grekoff, 1963 (pl. 3, figs 56–62; pl. 8, fig. 216), *P. accessa* Grekoff, 1963 (pl. 3, figs 63–68), *P. bicruciata* Grekoff, 1963 (pl. 3, figs 69–76; pl. 8, figs 218–221), *P. befotakaensis* Grekoff, 1963 (pl. 3, figs 77–80; pl. 8, figs 215, 217) and *Progonocythere* 2393 Grekoff, 1963 (pl. 4, figs 105–108), all from the Bathonian and Callovian of Madagascar, were assigned by Wienholz (1967) to *Fastigatocythere*.

important morphological characters. Valid taxa are written in bold	gical characters. Va	alid taxa are writt					
Genus	Size mm	Shape	Ornament	Muscle scars	Hinge	Anterior rpc	Eye tubercle
<i>Progonocythere</i> Sylvester-Bradley, 1948 Approximately 27 spp.	Mean L. 0.65, H. 0.38, W. 0.28, Range L. 0.45-0.85, H. 0.28-0-49, W. 0.14-0.42	Ovate, subovate, subrectangular, subquadrate ventro-laterally, tumid	Smooth, punctate, pitted, weakly reticulate, ventral longitudinal ribs, some shallow med. sulcus	Vertical/curved 4 adductors single heart-shaped/oval frontal single mandipular, some ? 2	Entomodont. Accommodation groove LV some spp.	Straight, well spaced usually 8, ranges to 16. Avestibulate	Eye-swelling and post-ocular sulcus in some species
<i>Glyptocythere</i> Brand and Malz, 1962 Approximately 40 spp.	Mean L. 0.87, H. 0.37, W. 0.32, Range L. 0.50–1.25, H. 0.32–0.43, W. 0.22–0.42	Egg-shaped to trapezoidal, laterally inflated, dorsal of LV arched	With or without strong reticulation with separate longitudinal and vertical ribs or low swellings	Curved/vertical 4 adductors one frontal and one mandibular scar	Strong entomodont	Straight, well spaced 9–12. Avestibulate	Absent
Majungaella Grekoff, 1963 Approximately 20 spp.	Mean L. 0-70, H. 046, W. 046, Range L. 0-73-0-98, H. 0-30-062, W. 0-39-0-53	Subtriangular to pyriforme, upturned posterodorsally, strongly inflated/dorsal view	Coarse punctae radiating in rows from dorsal margin then concentric. Ventral ribs. Anterior denticles	Vertical/oblique 4 adductors, single circular frontal scar and one oval mandibular	Entomodont	Originally curved and 14–20. Now up to 28. Some narrow vestib.	Eye tubercle and post-ocular sulcus
<i>Malzia</i> Bate, 1965 2 spp.	Mean L. 0-77, H. 0-44, W. 0-41, Range L. 0-69-0-85, H. 0-43-0-45, W. 0-38-0-44	Subquadrate, tapering to posterior margin	Smooth or punctate. Ventro- lateral part extended into 1 or 2 keel-like projections	Curved row of 4 adductors round antero-dorsal antennal scar. Mandibular scar not seen	Entomodont. Narrow, elongate, accommodation groove LV	Long, straight, well spaced. Approx. 8	Low eye tubercle. Not seen in all illustrated specimens
Fastigatocythere Weinholz, 1967 Approximately 12 spp.	Mean L. 0-68, H. 0-37, W. 0-78, Range L. 0-43-0-93, H. 0-25-0-50, W. 0-45-0-52	Subtriangular to subrectangular	Dorso-lateral with subvertical or inverted chevron ribs	Vertical row of 4 adductor scars and a rounded antennal scar. One mandibular scar	Entomodont	Well spaced, straight, ranging from 7-9	Eye tubercle and marked post- ocular sulcus

TABLE 2. The 12 genera of Progonocytherinae considered here, giving author, date of publication, number of species and details of size and most

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Approximately 25 Low, elongate eye swelling	Straight to slightly Eye tubercle and curved antero- post-ocular sulcus ventrally. Approx. 14	Straight to slightly Eye-tubercle and curved, 24-28 post-ocular sulcus	No data Eye tubercle and marked post- ocular sulcus	No data Eye tubercle and marked post- ocular sulcus	Straight, thick, Prominent eye well spaced. tubercle and post- Approx. 8 ocular sulcus	No data Absent?
Entomodont Ap	Lobodont Stra cu A	Entomodont	Entomodont No	Entomodont No	Strong entomodont Str w A.	Entomodont No
Curved row of round and approximate adductor scars	Curved row of 4 adductors with an anterocentral frontal scar	Row of 4 adductors, antennal scar heart- to V-shaped, one mandibular	No data	No data	 4 subvertical rounded-oval adductors, rounded antennal, ? divided mandibular scar 	No data
Concentric puncta. Anterior and posterior marginal denticles	Dorso-lateral ribs inverted chevron not projecting above dm. Ventro-lateral ribs parallel to venter	Coarsely punctate with rows diverging from the dorsal margin. Anterior marginal denticles	Subtriangular ribs in inverted chevron	Subtriangular ribs in inverted chevron which do not overreach dm. and broken by large tubercles	Reticulate	Pitted
Pyriform, upturned postero-dorsally, strongly convex in dorsal view	Subtriangular	Trapezoidal, pyriform, upturned postero- dorsally. Strongly convex dorsal view	Subtriangular, ovate, centrally tunid, somewhat pointed laterally in dorsal view	Subtriangular	Subquadrate to globose, dorsally umbonate, ventro-laterally tumid	Elongate oval, ventrolateral border slightly overhangs ventral margin
Mean L. 0-90, W. 0-57, Range L. 0-85-0-95, W. 0-55-0-60	Mean L. 0-60, H. 0-36, W. 0-35, Range L. 0-55-0-65, H. 0-35-0-37, W. 0-33-0-37	Mean L. 1-04, H. 0-67, Range L. 0-92-1-17, H. 0-58-0-76	Mean L. 0-69, H. 0-49, W. 0-37, Range L. 0-62-0-76, H. 0-37-0-45, W. 0-35-0-40	Mean L. 0-60, H. 0-33, W. 0-32, Range L. 0-55-0-67, H. 0-30-0-37, W. 0-30-0-35	Mean L. 044, H. 025, W. 025, Range L. 041–048, H. 020–024, W. 0-25	Mean L. 0-54, H. 0-28, W. 0-23, Range L. 0-49-0-68, H. 0-20-0-36, W. 0-22-0-24
Novocythere Rossi de Garcia, 1972 I sp.	Amicytheridea Bate, 1975 5 spp.	<i>Tickalaracythere</i> Krömmelbein, 1976 3 spp.	Glyptogatocythere Basha, 1980 2 spp.	Zergacythere Basha, 1980 2 spp.	<i>Dromacythere</i> Ware and Whatley, 1980 I sp.	<i>Strictocythere</i> Sheppard <i>in</i> Brand, 1990 2 spp.

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Genus -	Size mm	Shape	Ornament	Muscle scars	Hinge	Anterioi rpc	Eye tubercle
roga nacythere ylvester-Bradley, 1948 pproximately 27 spp	Mean 1 0.65, 11 0.38, W 0.28, Runge 1. 0.45-0.85, 11 0.28 0.49, W 0.14 0.42	Ovate, subovate, subrectangular, subquadrate ventro-laterally, tunnd	Smooth, punctate, pitted, weakly reticulate, ventral tongitudinal ribs, some shallow med suleus	Vertical/eurved 4 adductors single heart-shaped/oval frontal single mandibular, some 7 2	Enfomodont Accommodation groove LV some spp	Straight, well spaced usually 8, ranges to 16 Avestibulate	Eye-swelling and post-ocular sulcus in some species
<i>lyptocythere</i> rand and Malz, 1962 pproximately 40 spp	Mean L 0.87, 11 0.37, W 0.32, Ronge L 0.50 1.25, 11 0.32-0.43, W 0.22-0.42	Egg-shaped to tripezoidal, laterally inflated, dorsal of LV arched	With or without strong reticulation with separate longitudinal and vertical rubs or low swellings	Curved/vertical 4 adductors one frontal and one mandibular scar	Shong entontodont	Straight, well spaced 9-12 Avestihulate	Absent
l <i>ajungaella</i> rekoff, 1963 pproxintately 20 spp	Mean L (170), H 0.46, W 0.46, Range L 0.73-0.98, H 0.30-0.62, W 0.39-0.53	Subtriangular to pynforme, uptuined posterodorsally, strongly inflated/dorsal view	Coarse punctae radiating in rows from dorsal margin then concentric Ventral ribs Anterior dentricles	Vertical/oblique 4 adductors, single circular frontal scar and one oval mandibular	Entomodont	Originally eurved and 14-20. Now up to 28. Sonie narrow veslib	Lye tuberele and post-ocular sulcu
<i>นโลเม</i> แย, 1965 รอย	Nican L. 0.77, 11 0.44 W. 0.41, Range L. 0.69-0.85, 11 0.41-0.45, W. 0.38 0.44	Subquadrate, lapeniig to postenor margin	Smooth or punctate Ventro- lateral part extended (nto 1 or 2 keel-like projections	Curved row of 4 adductors round antero-dorsal anternal sear Mandibular sear not seen	Entomodont. Narrow, elongate, accommodation groove LV	Long, straight, well spaced Approx 8	Low eye tubercle Not veen in all iffustrated specimens
astigatocji (here Venholz, 1967 pproximately 12 spp	Me.in L 0.68, 11 0.37, W 0.78, Range L 0.43 0.93, 11 0.25–0.50, W 0.45-0.52	Subtriangular to subrectangular	Dorso-lateral with subvertical of inverted chevion ribs	Vertical row of 4 adductor scars and a rounded antennal scar One mandibular scar	Entomodant	Welf spaced, straight, ranging front 7-9	Eye tubercle and marked post- neular sulcus
n							
ovarjuhere ossi de Gareis, 1972 sp	Mean L. 0.90, W. 0.57, Range 1. 0.85 0.95, W. 0.55-0.60	Pynform, upturned postero-dorsally, strongly convex in dorsal view	Concentric puncta Anterior and posterior marginal denticles	Curved row of round and approximate adductor scars	Entemodont	Approximitely 25	Low, elongate eye swelling Eye tubercle and
unci theridea ate, 1975 spp	Mean L 0.60, H 0.36, W 0.35, Ringe L 0.55–0.65, H 0.35-0.37, W 0.33-0.37	Subinangular	Dorso-lateral ribs inverted chevion not projecting above dm Ventro-lateral ribs parallel to venter	Curved row of 4 adductors with an anterocentral frontal scar	Lobodont	Straight to slightly eurved antero- ventrally Approx, 14	post-ocular siileu
Fic <i>kalaracythere</i> Grömmelbein, 1976 Espp	Mean L. 1-04, H. 0.67, Range L. 0.92-1.17, H. 0.5X-0.76	Trapezoidal, pynform, upturned postero- dorsally Strongly convex dorsal view	Coarsely punctate with rows diverging from the dorsal margin Anterior marginal dentieles	Row of 4 adductors, antennal scat heart: to V-shaped, one mandibular	Entomodont	Straight to slightly curved, 24-28	Eye-tuberele and post-ocular suleu
Glyptogatorythete Basha, 1980 2 spp.	Mesn L 0.69, H 0.49, W 0.37, Range L 0.62–0.76, H 0.37–0.45, H 0.37–0.45,	Subtriangular, osate, centrally tumid, somewhat pointed laterally in doisal view	Subtriangular rabs in inverted chevron	No data	Entomodont	No data	Eye tuberele and marked post- ocular suleus
Zergaci there Basha, 1980 2 spp	W 0.35-0.40 Mean L 0.60, H 0.33, W 0.32, Range L 0.55-0.67, H 0.30.0.37, W 0.30.0.35	Subtrangular	Subtriangular ribs in inverted ehevion which do not overreach dm. and broken by large tubercles	No data	Entomodont	No data	Eye tubercle and marked post- ocular sulcus
<i>Dromacythere</i> Ware and Whatley, 1980 I sp	W 0.40 0.35 Mean L 0.44, H 0.25, W 0.25, Range L 0.41-0.48, H 0.20-0.24, W 0.25	Subquadrate to globose, dorsally umbonate, ventro-laterally tumid	Reticulate	 subvertical rounded-oval adductors, rounded antennal, 7 divided mandibular scar 	Strong entomodont	Straight, thick, well spaced. Approx 8	Prominent eye tuberele and po ocular suleus
Structory there Sheppard in Brand, 1990 2 spp	Mean L. 0.54, 11 0.28, W 0.23, Range L. 0.49-0.68, 11, 0.20-0.36,	Elongate oval, ventrolateral border slightly overhangs ventral margin	Pitted	mandibular scar No data	Entomodont	No data	Absent?

TABLE 2. The 12 genera of Progenocytherinae considered here, giving author, date of publication, number of species and details of size and most important morphological characters. Valid taxa are written in bold.

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7. *Progonocythere falcula* Grekoff, 1963 (pl. 4, figs 88–91), from the Middle Callovian of Madagascar, probably belongs in *Fastigatocythere* Wienholz because of its triangular and posteriorly acuminate shape and post-ocular sulcus.

8. *Progonocythere mundula* Grekoff, 1963 (pl. 4, figs 92–95), from the Middle Callovian of Madagascar, certainly belongs in *Majungaella* Grekoff.

9. Progonocythere? juglandica (Jones) sensu Oertli 1963 (pl. 28, fig. 2b), from the Bathonian of France, certainly belongs in Fastigatocythere Wienholz.

10. Progonocythere? aff. anoda Peterson subsp. ancestor (Oertli) in Maync, 1966 (pl. 10, fig. 48), from the Bathonian of Israel, belongs in *Fastigatocythere* Wienholz (= F. bakeri (Basha) sensu Rosenfeld et al. (1987, pl. 3, figs 1–8)).

11. Progonocythere? posteriolumulis Blaszyk, 1967 (pl. 20, figs 11–13; text-fig. 20) from the Middle Bathonian of Poland, seems to have an antimerodont hinge and is much too elongate-acuminate posteriorly to be *Progonocythere*. In shape, it resembles *Aaleniella* Plumhoff.

12. Progonocythere (Majungaella) nematis Dingle in Dingle and Klinger, 1972 (pl. 18, fig. a), from the Upper Jurassic of South Africa, belongs in Majungaella Grekoff.

13. Progonocythere (Majungaella) brentonensis Dingle in Dingle and Klinger, 1972 (fig. 4; pl. 16, figs f-i; pl. 17, figs a-c), from the Upper Jurassic of South Africa, belongs in neither Progonocythere nor Majungaella, which we regard as discrete taxa. This species belongs in Fastigatocythere Wienholz, because of its triangular and posteriorly acuminate shape, its post-ocular sulcus and (although weakly developed) its inverted chevron ornament.

14. Progonocythere (Majungaella) reticulata Dingle in Dingle and Klinger, 1972 (pl. 17, figs d-i) (non Progonocythere reticulata Bate, 1963 which is a true Progonocythere) is from the Upper Jurassic of South Africa. From its shape and outline, we consider it to belong in Afrocytheridea Bate.

15. Progonocythere spitiensis Jain and Mannikeri, 1975 (pl. 1, figs F–H), from the Upper Jurassic of India, certainly belongs in *Majungaella* Grekoff.

16. Progonocythere befotkaensis (sic) Grekoff sensu Guha (1976, pl. 2, figs 12a-b, 13), from the Upper Jurassic of Kutch, India, belongs in Fastigatocythere Wienholz.

17. Progonocythere plettenbergensis McLachlan, Brenner and McMillan, 1976 (pl. 16, figs 3–7), from the Hauterivian of well PB-A/1 (South Africa), belongs in *Fastigatocythere* Wienholz.

18. ? *Progonocythere* sp. A McLachlan *et al.*, 1976 (pl. 16, figs 8–10), from the ?Berriasian–Lower Valanginian of well PB-A/1 (South Africa), belongs in *Fastigatocythere* Weinholz.

19. Progonocythere reticulata Dingle in McLachlan et al., 1976 (pl. 16, figs 1–2), from the Valanginian of well PB-A/1 (South Africa), should be included in *Afrocytheridea* Bate.

20 Progonocythere brentonensis Dingle in McLachlan et al., 1976 (pl. 15, figs 18–21), from the Valanginian of PB-A/1 well (South Africa), belongs in Fastigatocythere Wienholz.

21. Progonocythere neuquenensis Musacchio, 1978 (pl. 2, figs 14–18), from the Middle Callovian of Argentina, could, by its shape and outline, be tentatively included in *Fastigatocythere* Wienholz.

22. Progonocythere cf. reticulata Dingle sensu Musacchio, 1981 (pl. 2, fig. 12), from the Valanginian of Argentina, is similar to and possibly conspecific with Dingle's species above and is, therefore, considered to belong in Afrocytheridea Bate.

23. Progonocythere pyramida, P. ramosa and P. schuleridiformis Wasfi, El Sweify and Abdelmalik, 1982 (pl. 5, respectively figs 54–55, figs 46–48 and fig. 37), from the Bathonian and Callovian of the Gulf of Suez, Egypt, do not belong in *Progonocythere* but are placed, tentatively (due to poor descriptions and illustrations) in *Fastigatocythere* Weinholz (*pyramida, ramosa*) and *Galliaecytheridea* Oertli (*schuleridiformis*).

24. Progonocythere A Kielbowicz et al., 1983 (pl. 6, fig. 12) is from the Valanginian of the Argentine part of the Austral Basin (southern Argentina). According to the illustrations (there is no description), it does not belong to *Progonocythere*; its clearly triangular outline and strong ventral rib suggest that it should be tentatively included in *Fastigatocythere* Wienholz.

25. *Progonocythere? freudni* Rosenfeld and Raab, 1984 (pl. 9, figs 10–16), from the Neocomian of Israel, is much too elongate and acuminate posteriorly. It also has a chevron-type ornament which is not typical of *Progonocythere*, and could possibly be included in *Neocythere* Mertens.

26. Progonocythere implicata Ljubimova and Mohan in Kulshreshtha et al., 1985 (fig. 7.11–7.12), from the Callovian–Oxfordian of India, more closely resembles Afrocytheridea Bate.

27. Progonocythere banniensis Neale and Singh, 1985 (pl. 3, fig. 2), from the Callovian of India, more closely resembles Afrocytheridea Bate.

Doubtful species of Progonocythere. Progonocythere retusa Grekoff, 1963, from the Middle

Bathonian of Madagascar, has, according to the author, chevron-type ornament. Since this feature is not visible in the illustrations (pl. 3, figs 81–87) and the lateral surface is smooth with isolated punctation, we have provisionally retained this species in *Progonocythere* despite the fact that it is rather elongate, although not so elongate as species such as *P. polonica* Blaszyk.

Progonocythere cf. *letruelensis* (Rohr, 1976) *in* Malz *et al.* 1985 (pl. 6, fig. 57), from the Bajocian–Callovian of Sardinia, seems to be too strongly tumid to belong in *Progonocythere*; it may belong in *Klieana* Martin.

Progonocythere sp. Rosenfeld *et al.* 1987 (pl. 3, fig. 11), from the Oxfordian of Israel and *Progonocythere kutchensis* Guha, 1976 (pl. 1, figs 2a–b, 3), from the Upper Jurassic of India, are doubtful species due to their incomplete description and poor illustration.

Synonymized genera. We consider that the genus *Malzia* Bate, 1965 (p. 110, pl. 9, figs 5–8; pl. 10, figs 1–3), from the British Bajocian, is merely *Progonocythere* with a ventro-lateral keel-like prolongation, similar to that of *Progonocythere yonsnabensis* Bate, 1965 (pl. 12, figs 5–14; pl. 13, figs 1–4) from the Bajocian of the Grey Limestone Series [= Scarborough Formation], Yorkshire. Similarly, we regard *Strictocythere* Sheppard *in* Brand, 1990 (p. 207, pl. 13, figs 8–15), from the Upper Bathonian of Europe, as merely a more elongate-oval *Progonocythere*. We have emended the diagnosis of *Progonocythere* to include the species of these synonymized genera.

Emended diagnosis of Progonocythere *Sylvester-Bradley*, *1948.* Progonocytherinae with ovate to elongate-ovate, subrectangular or subquadrate shape; ventro-laterally tumid; with or without ventro-lateral keel-like prolongations extending below the ventral surface; smooth, punctate to pitted and weakly reticulate; ventral surface with longitudinal ribs, often shallow vertical median sulcus. Eye swelling and post-ocular sulcus present in some species. Entomodont hinge with accommodation groove in left valve in some species. Anterior pore canals usually eight but ranging to 16. Muscle scars comprising vertical or curved row of four adductors and heart or oval shaped frontal scar; usually one mandibular but two reported for some species. Left valve larger than right. Sexually dimorphic; males longer, less high and less tumid than females.

Distribution. Progonocythere ranges from the Bajocian to Oxfordian, although Bate (1977, p. 234) cited a species from the Kimmeridgian of Spain. It has a geographical range largely restricted to the Northern Hemisphere, particularly Britain and Europe. Ascoli (1988, p. 25) recorded, but did not illustrate, *P. polonica* and *P. aff. rugosa* from the Bathonian of offshore eastern Canada. Two species, *P. laeviscula* and *P. prolongata* [Ex *Strictocythere*], from the Callovian–Oxfordian of India and Madagascar, and the Bajocian of Australia respectively, are known Southern Hemisphere species.

Valid species. We consider the following species (listed in date order) to be valid members of *Progonocythere.* In this, and all subsequent lists of valid species, an asterisk indicates a new combination:

- P. stilla Sylvester-Bradley, 1948; Bathonian, Britain (Pl. 1, figs 1-3)
- *P. polonica Blaszyk, 1959; Bathonian Poland (Ex Strictocythere (Text-fig. 11-J)
- P. ogrodizieniecensis Blaszyk, 1959; Bathonian, Poland
- P. laeviscula Ljubimova, Guha and Mohan, 1960; Callovian–Oxfordian, India
- P. cristata Bate, 1963; Bajocian, Britain
- P. reticulata Bate, 1963; Bajocian, Britain
- P. multipunctata Whatley, 1964; Oxfordian, Britain
- P. parastilla Whatley, 1964; Oxfordian, Britain
- P. acuminata Bate, 1965; Bajocian, Britain
- *P. bicarinata (Bate, 1965); Upper Bajocian, England (Ex Malzia) (Pl. 1, figs 8–9)
- P. polita Bate, 1965; Bajocian, Britain
- *P. unicarinata (Bate, 1965); Upper Bajocian, England (Ex Malzia)

- P. yonsnabensis Bate, 1965; Bajocian, Britain
- P.? convexa Blaszyk, 1967; Bathonian, Poland
- P. praepolonica Dreyer, 1967; Bajocian, Germany
- P. callovica Wienholz, 1967; Callovian, Germany
- P. laevigata Bate, 1967; Bathonian, Britain
- P. rugosa Bate, 1967; Bathonian, Britain
- P. triquetra Bate, 1967; Bathonian, Britain
- P. lacazensis Rohr, 1976; Bathonian, France
- P. laeviscula Ljubimova, Guha and Mohan, 1960 sensu Kulshreshtha et al. 1985; Callovian–Oxfordian, India P. postangusta (Sheppard) sensu Dèpêche, 1985; Middle Bathonian, France
- *P. honigsteini* Rosenfeld and Gerry *in* Rosenfeld *et al.* 1987; Bathonian, Egypt
- *P.* aff. *parastilla* Whatley, 1964 *in* Rosenfeld *et al.* 1987; Oxfordian, Egypt
- 1. an. parasitia whatey, 1904 in Rosenfeld et al. 1967, Oxfordian, Egypt
- Progonocythere sp. Dèpêche et al., 1987; Bajocian-Bathonian, Saudi Arabia
- P. polonica recta Brand, 1990; Upper Bathonian, Germany
- Progonocythere sp. Rosenfeld and Honigstein, 1991; Callovian, Israel
- **P. prolongata* (Chapman, 1904) *in* Malz and Oertli 1994; Lower Bajocian, Australia (Ex *Loxoconcha elongata* Chapman, 1904; Ex *Strictocythere*)

Glyptocythere Brand and Malz, 1962

This genus was described by Brand and Malz (1962) based on six species (type species *Glyptocythere tuberodentina*) with entomodont hinge and egg-shaped to trapezoidal valves in lateral view, strongly inflated lateral surface and an ornament with or without strong reticulation, and vertical ribs or only

EXPLANATION OF PLATE 1

- Figs 1–3. *Progonocythere stilla* Sylvester-Bradley; Bathonian, Langton Herring, Dorset, England; The Natural History Museum, Department of Palaeontology. 1–2, 41908, holotype; right valve. 1, external view. 2, internal view. 3, paratype, 41909, external view. All × 64.
- Figs 4-6. *Glyptocythere tuberodentina* Brand and Malz; Bajocian, Germany; Senckenberg Museum, Department of Palaeontology, Frankfurt-am-Main. 4, SMF Xe 4299, holotype; female, left valve, external view. 5, SMF Xe 4306, paratype; female, right valve, internal view. 6, SMF Xe 4306; female, right valve, external view. All × 50.
- Fig. 7. *Majungaella perforata* Grekoff; Portlandian, Madagascar; Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris; H275, holotype; female, right valve, external view; × 54.
- Figs 8–9. *Progonocythere bicarinata* (Bate) (Ex *Malzia*); Upper Bajocian, Yorkshire, England; The Natural History Museum, Department of Palaeontology; Io 1797; female, left valve. 8, external view. 9, dorsal view. Both × 59.
- Figs 10–14. Fastigatocythere juglandica (Jones) (Ex Progonocythere Whatley; Ex Cythere Jones), Upper Bathonian, Oxfordshire. Aberystwyth Micropalaeontological Museum. 10, RCW/Bath/107; female, left valve, external view. 11, RCW/Bath/105; female, right valve, external view. 12, RCW/Bath/109; male, right valve, external view. 13, RCW/Bath/107; female, left valve, internal view. 14, RCW/Bath/102; male, left valve, external view. All × 57.
- Figs 15–16. Majungaella santacruziana (Rossi de García, 1972) (Ex Novocythere); Aptian–Albian, southern Argentina; topotype from collections of Dirección Nacional Servicio Geológico, Buenos Aires, and now in micropalaeontological collections of Division de Paleozoologia Invertebrados, Museo de La Plata, La Plata, Argentina. From type level, borehole Sc-1, at 903–918m, Santa Cruz, Argentina; MLP 0271; female, left valve. 15, external view. 16, internal view. Both × 47.
- Fig. 17. Fastigatocythere ihopyensis (Grekoff, 1963) (Ex Amicytheridea Bate; Ex Procytheridea Grekoff); Middle Callovian, Tanzania. The Natural History Museum, Department of Palaeontology; Io 6251; female, left valve, external view; × 70
- Figs 18–20. Fastigatocythere triangulata (Bate, 1975) (Ex Amicytheridea); Callovian, Tanzania; The Natural History Museum, Department of Palaeontology. 18, Io 6116; male, right valve, external view, × 64. 19, Io 6115; male, right valve, internal view; × 85. 20, Io 6114; female, left valve, external view; × 69.

PLATE 1



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low swellings. In 1966, they reviewed the genus and added 16 new species. It was considered to be typical of the Bajocian and Bathonian, with a geographical distribution extending from Britain, south-eastwards to the Ukraine (Permjakova 1970) and Uzbekistan (Masumov 1973, see *Macrodentina aspera*, pl. 9, fig. 2)

We consider that the following taxa are best removed from the genus and accommodated elsewhere:

1. *Glyptocythere polita* Bate, 1965 (pl. 5, figs 8–11; pl. 6, figs 1–9), from the Bajocian of Britain, closely resembles *Progonocythere* in shape and in its smooth shell surface, with shallow median sulcus, and its convex ventrolateral extension of the carapace like a thin keel. We have included this species in *Progonocythere* although we are well aware that end members of the two genera are morphologically very similar and that convergence between the two is likely.

2. *Glyptocythere juglandica* (Jones) Bate, 1967 (pl. 4, fig. 9), from the Bathonian of Britain, is now *Fastigatocythere* Wienholz.

3. *Glyptocythere? malzi* Dèpêche, 1973 (pl. 2, figs 9–13), from the Bathonian of France, was later considered by her to be *Kinkelinella* Martin, 1960 (see Dèpêche 1985, pl. 30, fig. 15); we agree.

4. *Glyptocythere lumiensis* Basha, 1980 (pl. 2, figs 5–9), from the Bathonian of Jordan, is *Fastigatocythere* Wienholz.

5. *Glyptocythere*? sp. Malz *et al.*, 1985 (pl. 6, figs 6–8), from the Bathonian of north-west Sardinia, and only figured, more closely resembles *Progonocythere*.

6. *Glyptocythere oblonga* (Basha) *sensu* Rosenfeld and Gerry *in* Rosenfeld *et al.* 1987 (pl. 4, figs 7–8), from the Bajocian–Bathonian of Israel, should be included in *Fastigatocythere* Wienholz.

Diagnosis of Glyptocythere *Brand and Malz*, 1962. At present, we do not regard it as necessary to amend the original diagnosis of the genus except to ensure that it includes rather elongate species such as *G. guembeliana* (Jones) in which the ornament is very feeble or almost smooth. A translated synopsis of the original diagnosis is given below.

Carapace medium to large, egg-shaped to trapezoidal in lateral view; subrectangular to elliptical in dorsal view with end marginal borders clearly distinct from strongly inflated lateral surface. Left valve larger than right valve. Dorsal margin medianly vaulted in left valve, overhung by dorsolateral surface. Ocular features absent. Ornament with or without strong reticulation with separate longitudinal and vertical ribs or low swellings. Avestibulate. Marginal area wide. Usually nine but up to 12 radial pore canals anteriorly, straight, widely spaced and unbranched; three to five posteriorly. Normal pore canals tend to open through elevations in ornament. Hinge entomodont.

Valid species. We consider the following species to be valid members of *Glyptocythere*:

- G. auricula Brand and Malz, 1962; Bathonian, Germany
- G. dorsicostata Brand and Malz, 1962; Bajocian, Germany
- G. rudimenta Brand and Malz, 1962; Bajocian, Germany
- G. tenuisulcata Brand and Malz, 1962; Bajocian, Germany
- G. tuberodentina Brand and Malz, 1962; Bajocian, Germany (Pl. 1, figs 4-6)
- G. tuberosa Brand and Malz, 1962; Bathonian, Germany
- G. costata Bate, 1965; Bajocian, Britain
- G. scitula Bate, 1965; Bajocian-Bathonian, Britain
- G. comes Brand and Malz, 1966; Bathonian, Germany
- G. concentrica Brand and Malz, 1966; Bajocian, Germany
- G. hieroglyphica Brand and Malz, 1966; Bajocian, Germany
- G. interrete Brand and Malz, 1966; Bajocian, Germany
- G. meandrica Brand and Malz, 1966; Bajocian, Germany
- G. perpolita Brand and Malz, 1966; Bajocian, Germany
- G. plicata Brand and Malz, 1966; Bajocian, Germany
- G. praecursor Brand and Malz, 1966; Bajocian, Germany
- G. regulariformis Brand and Malz, 1966; Bajocian, Germany
- G. rugosa Brand and Malz, 1966; Bajocian, Germany

- G. similis Brand and Malz, 1966; Bajocian-Bathonian, Germany
- G. sowerbyi Brand and Malz, 1966; Bajocian, Germany.
- G. trinodis Brand and Malz, 1966; Bajocian, Germany
- G. tuscilla Brand and Malz, 1966; Bajocian, Germany
- G. umbonata Brand and Malz, 1966; Bajocian, Germany
- G. obtusa Lutze, 1966; Bathonian, Germany
- G. perpolita magna Blaszyk, 1967; Bajocian-Bathonian, Germany
- G. tuberosa angularis Blasyzk, 1967; Bajocian-Bathonian, Germany
- G. guembeliana (Jones) in Bate 1967; Bathonian, Britain
- G. oscillum (Jones and Sherborn), in Bate, 1969; Bathonian, Britain
- G. persica (Jones and Sherborn), in Bate, 1969; Bathonian, Britain
- G. aspera (Khaborava) in Permjakova, 1970; Middle Jurassic, Dnieper Don Depression, Russia
- G. crassicostata Permjakova, 1970; Middle Jurassic, Dnieper Don Depression, Russia
- G. losoviensis Permjakova, 1970; Middle Jurassic, Dnieper Don Depression, Russia
- G. multa Permjakova, 1970; Middle Jurassic, Dnieper Don Depression, Russia
- G. medisculata Blaszyk, 1972; Bajocian, Poland
- G. posterocostata Blaszyk, 1972; Bajocian, Poland
- Glyptocythere sp. Blaszyk, 1972; Bajocian, Poland
- G. penni Bate and Mayes, 1977; Bathonian, Britain
- Glyptocythere sp. Bate, 1978; Bajocian, Britain
- G. raasayensis Stevens, 1985; Bajocian, Isle of Raasay, Scotland
- G. cf. dorsicostata Brand and Malz sensu Dèpêche, 1985; Bathonian, France

Majungaella Grekoff, 1963

The genus *Majungaella* was described by Grekoff (1963) from the Upper Jurassic and Lower Cretaceous of the Majunga Basin, Madagascar with his new Kimmeridgian–Portlandian species, *M. perforata*, as type. He described a second new Madagascan species, *M. nematis*, ranging from the Portlandian to Valanginian. Subsequently, species of *Majungaella* have been described from the Callovian–Portlandian and Albian of Tanzania (Bate and Bayliss 1969); South Africa (Brenner and Oertli 1976; Valicenti and Stephens 1984); the Upper Cretaceous of Australia (Bate 1972); the Lower and Upper Cretaceous of Argentina (Rossi de García and Prosperpio 1980; Kielbowicz *et al.* 1983), and the Albian of the Falkland Plateau (Dingle 1984). *Majungaella* aff. *nematis* Grekoff is cited (not figured) from probable Valanginian strata in southern Chile (Sigal *et al.* 1970). According to its geographical distribution, *Majungaella* is considered to be a genus typical of the Southern Hemisphere.

In the present review, we have encountered several species which we consider would be best removed from the genus and accommodated elsewhere:

1. *M. queenslandensis* Krömmelbein, 1975 (pl. 2, figs 4–6), *M. margaritata* Krömmelbein, 1975 (pl. 1, figs 1–2) and *Majungaella* sp. A Krömmelbein, 1975 (pl. 1, fig. 3), from the Albian–Cenomanian of Australia, were recently described as the new genus *Exposterocythere* Whatley, Ballent and Maybury, 1995b.

2. *Majungaella*? sp. B Krömmelbein, 1975, from the Albian–Cenomanian of Australia, seems be a juvenile specimen of *Exposterocythere queenslandensis* (Krömmelbein).

3. Majungaella verseyi Neale, 1975 (pl. 8, fig. 5; pl. 14, fig. 3; text-fig. 2b), from the Santonian of Australia, is placed in *Exposterocythere* Whatley, Ballent and Maybury, 1995b.

4. *Majungaella brentonensis* (Dingle) *sensu* Guha 1976 (pl. 3, fig. 16a-b), from the Upper Jurassic of Kutch, India, belongs to *Fastigatocythere* Wienholz.

5. *Majungaella*? *minuta* Swain, 1976 (pl. 1, figs 19–21, 23), from the Aptian/Albian of DSDP, north-west Atlantic, has a hemimerodont hinge and is very much smaller (L = 0.36 mm) than all other species. This is possibly a *Procytheridea* Peterson.

6. *M.* cf. queenslandensis Krömmelbein in Dingle 1984 (figs 170–187) is conspecific with Majungaella sp. A Dingle, 1972 (fig. 4), from the Aptian/Albian of South Africa, and both are included in *Exposterocythere*.

7. *Majungaella*? sp. 327/16 Dingle, 1984 (fig. 18A-c), from the Middle Albian of South Africa, which seems to have an antimerodont hinge, should be referred to the Cytherideidae

Doubtful species of Majungaella. *Majungaella? hemigymmae* Brenner and Oertli *in* Dingle 1984 (fig. 17F), from the Aptian of South Africa, is only a fragmentary carapace, and it is not possible, therefore, to assign it to any genus with certainty.

Synonymized genera. In the original description by Grekoff (1963), Majungaella is diagnosed as having a robust carapace with surface coarsely punctate and an anterior marginal zone with 14–20 marginal pore canals. Dingle *in* Dingle and Klingler (1972) and Bate (1975) considered that these canals increase in number from 14–20 in the Jurassic, to 28–30 in the Cretaceous. Krömmelbein (1975) removed from *Majungaella* those Upper Cretaceous species having an increased number of anterior marginal pore canals (24–28) and a distinctive upturned postero-dorsal margin, and placed them in his new genus *Tickalaracythere*. Rossi de García (1972) described *Novocythere* from the Aptian–Albian of southern Argentina, with nearly 25 anterior marginal pore canals but all other characters of her genus appear to be the same as *Majungaella*. We consider that an increase in number of anterior marginal pore canals is not a character sufficient to separate genera; on the contrary, it is a signal of evolution within a genus (cf. within the schulerideinid lineage *Eoschuleridea–Aequaecytheridea*). We have, therefore, amended the diagnosis of *Majungaella* to accommodate the species of both *Tickalaracythere* and *Novocythere*.

Emended diagnosis of Majungaella *Grekoff*, 1963. Progonocytherinae with robust carapace; pyriform, subtriangular to trapezoidal in lateral view and postero-dorsally upturned; strongly convex in dorsal view. Lateral surface ornamented by coarse punctae in concentric pattern; ventral surface with longitudinal ribs. Marginal denticles common especially anteriorly. Left valve larger than right. Eye tubercle and shallow post-ocular sulcus present. Hinge entomodont. Anterior marginal pore canals 14–28 or more in number. A very narrow anterior vestibulum may be present.

Stratigraphical range. Callovian to Maastrichtian.

Valid species. We consider the following species to be valid members of Majungaella:

**M. mundula* (Grekoff, 1963); Middle Callovian, Madagascar (Ex *Progonocythere*)

M. nematis Grekoff, 1963; Valanginian, Madagascar

M. perforata Grekoff, 1963; Portlandian, Madagascar (Pl. 1, fig. 7)

M. pyriformis Bate and Bayliss, 1969; Albian, Tanzania

M. annula Bate, 1972; Santonian and Campanian, Australia

**M. santacruziana* (Rossi de García, 1972); Aptian–Albian, southern Argentina (Ex *Novocythere*) (Pl. 1, figs 15–16)

- M. kimmeridgiana Bate, 1975; Kimmeridigian, Tanzania
- M. oxfordiana Bate, 1975; Upper Oxfordian, Tanzania

M. praeperforata Bate, 1975; Kimmeridigian, Tanzania

M. scheibnerovae (Krömmelbein, 1975); Aptian–Albian, Australia. This species is probably a junior synonym of *M. santacruziana* (Rossi de García)

*M. ticka (Krömmelbein, 1975); Aptian-Albian, Australia (Ex Tickalaracythere) (Text-fig. 1A-D)

M. bifurcata Brenner and Oertli, 1976; Valanginian-Hauterivian, South Africa

M. hemigymnae Brenner and Oertli, 1976; Hauterivian, South Africa

- M. perforata Grekoff in Guha, 1976; Upper Jurassic, India
- M. nematis Grekoff in Guha, 1976; Upper Jurassic, India

M. australis Rossi de García and Proserpio, 1980; ?Upper Campanian-Lower Maastrichtian, southern Argentina

Majungaella A Kielbowicz *et al.*, 1983; Valanginian, Southern Argentina (which we consider to be conspecific with *M. praehemigymnae* Valicenti and Stephens)

M. praehemigymnae Valicenti and Stephens, 1984; Valanginian, South Africa

M. uitenhagensis (Dingle) in Valicenti and Stephens, 1984; Valanginian-Hauterivian, South Africa

M. cf. perforata Grekoff in Rosenfeld and Raab, 1984; Neocomian, Israel

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M. mundula (Grekoff) *in* Kulshreshtha *et al.*, 1985; Callovian–Oxfordian, India *M. biswasi* Neale and Singh, 1986; Oxfordian, India

Malzia Bate, 1965

The genus *Malzia* was described by Bate (1965, p. 110), from the Upper Bajocian of England, as Progonocytherinae with subquadrate carapace, tapering to posterior margin and with anterior and posterior compressed margins. The ventro-lateral border extended into keel-like projections and there was a low eye swelling. The hinge was entomodont, 2nd anterior marginal pore canals numbered approximately eight.

This genus was erected with two species: the type species, *M. bicarinata* Bate (1965, p. 111, pl. 9, figs 5–8; pl. 10, figs 1–3; text-figs 11–14) having two ventro-lateral keels, and *M. unicarinata* Bate (1965, p. 113, pl. 10, figs 4–10; pl. 11, figs 1–4; text-fig. 15) with only one. Although *Malzia* with its keels somewhat resembles *Marslatourella* Malz, the resemblance is entirely superficial since the latter genus belongs to the Exophthalmocytheridae and differs in hingement and other important internal details.

Comparison of the illustrations of *Malzia* with those of *Progonocythere yonsuabensis* Bate, 1965 (p. 116, pl. 12, figs 5–14; pl. 13, figs 1–4; text-figs 16–19) and *Progonocythere acuminata* Bate, 1965 (p. 114, pl. 2, figs 5–10; pl. 12, figs 1–4), both from the Bajocian of England, shows that *Malzia* is merely *Progonocythere* with ventro-lateral keel-like projections. The amended diagnosis of *Progonocythere* (see above) includes *Malzia*.

Fastigatocythere Wienholz, 1967

This genus was based mainly on species with inverted chevron-type ornament, pronounced postocular sulcus and entomodont hinge. In addition to the type species, *F. rugosa* from the Callovian of north-west Germany, and *Progonocythere juglandica juglandica* (Jones) from the Middle Jurassic of Europe, Wienholz (1967) also included the following Middle Jurassic Madagascan species of Grekoff (1963): *Progonocythere accessa*, *P. bicruciata*, *P. befotakaensis*, *Progonocythere* 2393 and *P. juglandica malgachica*. Since 1967, there have been many more records of the genus. In our opinion, those which follow should be excluded.

1. Lophocythere interrupta Triebel, 1951 (pl. 47, figs 35–41) from the Callovian of Europe, has been placed by a number of authors in *Fastigatocythere*. However, we agree with Whatley (1970, p. 335) that it conforms to the diagnosis of *Lophocythere* Sylvester-Bradley and should certainly be retained there.

2. Dèpêche (1973, p. 216) relegated *Fastigatocythere* to the position of a subgenus of *Lophocythere* Sylvester-Bradley but we retain it here as a distinct genus. Both *Lophocythere (Fastigatocythere) bessinensis* Dèpêche, 1973, pl. 1, figs 3–8 and *Lophocythere (Fastigatocythere) rimosa* Dèpêche, 1973, pl. 1, figs 9–13), from the Lower Bathonian of France belong, in our opinion, to *Neurocythere* Whatley.

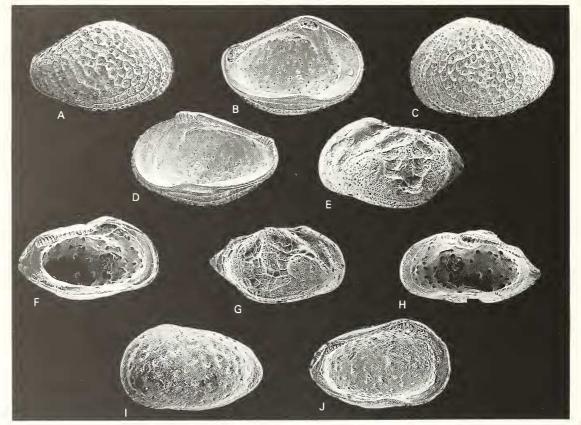
3. *Fastigatocythere? grekoffi* Brenner and Oertli, 1976 (pl. 6, fig. 5–12; pl. 8, fig. 6), from the Valanginian of South Africa, is certainly *Majungaella* Grekoff.

4. *Fastigatocythere interrupta interrupta* (Triebel, pl. 4, figs 5–6) and *F. interrupta* subsp. A (Lutze), pl. 4, figs 8–9, both *in* Herngreen *et al.* (1983–1984), from the Middle Callovian of the eastern Netherlands should be retained in *Lophocythere* Sylvester-Bradley. (See 1. above).

5. *Fastigatocythere naftaliensis* Rosenfeld and Raab, 1984 and Rosenfeld *et al.* 1988, from the Lower Cretaceous of Israel, seems to have an antimerodont hinge and possibly belongs to *Neocythere* Mertens.

Doubtful species of Fastigatocythere. *Fastigatocythere*? sp. Neale and Singh, 1985 (pl. 2, fig. 11), from the Oxfordian of India, is particularly difficult to place generically due to the inadequacy of its illustration.

Synonymized genera. The diagnosis of Fastigatocythere is herein amended to accommodate the species of Amicytheridea Bate; Glyptogatocythere Basha; and Zerqacythere Basha.



TEXT-FIG. 1. A-D, Majungaella ticka (Krömmelbein) (Ex Tickalaracythere); Australian Geological Survey Organisation, Canberra. A, D, CPC 13868, holotype; male, right valve, external (A) and internal (D) views; × 34 and × 39. B-C, CPC 13869, paratype; female, left valve, internal (B) and external (C) views; × 43. E-H, Dromocythere sagittata Ware and Whatley, 1980; Upper Bathonian, Oxfordshire, England; The Natural History Museum, Department of Palaeontology. E-F, OS 11337, holotype; female, left valve, external (E) and internal (F) views; × 102. G, OS 11338, paratype; female, right valve, external view; × 91. H, OS 11343, paratype; female, right valve, internal view; × 91. I-J, Progonocythere polonica Blaszyck, 1959 (Ex Strictocythere); Bathonian, France; British Geological Survey, Keyworth, Nottingham, England. 1, MPK 3683; female, left valve, external view; × 59. J, MPK 3684; female, left valve, internal view; × 59.

Emended diagnosis of Fastigatocythere *Wienholz, 1967.* Progonocytherinae with subtriangular to subrectangular lateral outline; ornamented by ribs in inverted chevron which overreach dorsal margin and may be broken up centrally into coarse reticulation creating prominent tubercles. Ventrally punctate or with ribs parallel to ventral margin. Eye tubercle and marked post-ocular sulcus. Left valve larger than right. Anterior marginal pore canals normally seven to nine, but range up to 14. Avestibulate. Frontal scar anterodorsal in position, usually circular.

Distribution. Fastigatocythere Wienholz is a typical Middle and Upper Jurassic genus with a wide stratigraphical and geographical distribution. In the Northern Hemisphere, it has been recognized mainly from the Bathonian–Kimmeridgian of Britain, continental Europe, Egypt, Jordan and Saudi Arabia; it is also recorded (not illustrated) from the Callovian and Oxfordian of offshore eastern Canada (Ascoli 1988, p. 26). In the Southern Hemisphere, it is recognized from the Bathonian–Kimmeridgian of East and South Africa, Madagascar and India, and also from the Lower Bajocian of Australia. From the Middle Callovian of Argentina, there is one species

(Progonocythere neuquenensis Musacchio) which, at present, we assign tentatively to Fastigatocythere Weinholz.

Valid species. We consider the following species to be valid members of Fastigatocythere:

F. rugosa Wienholz, 1967; Lower Callovian, Germany

*F. accessa (Grekoff, 1963); Bathonian-Callovian, Madagascar (Ex Progonocythere)

*F. bicruciata (Grekoff, 1963); Bathonian–Callovian, Madagascar (Ex Progonocythere)

*F. befotakaensis (Grekoff, 1963); Bathonian–Callovian, Madagascar (Ex Progonocythere)

*Fastigatocythere 2393 (Grekoff, 1963); Bathonian-Callovian, Madagascar (Ex Progonocythere)

F. juglandica juglandica (Jones) in Wienholz, 1967; Middle Jurassic, Europe and Madagascar (Pl. 1, figs 10-14)

F. juglandica malgachica (Grekoff, 1963); Bathonian-Callovian, Madagascar

F. aff. brentonensis (Dingle) in Bate, 1975; Middle-Upper Kimmeridigian, Tanzania

*F. ihopyensis (Grekoff) in Bate 1975, Bathonian–Callovian, East Africa, India and Madagascar (Ex Amicytheridea) (pl. 1, fig. 17)

*F. triangulata (Bate, 1975); Callovian, East Africa and Madagascar (Ex Amicytheridea)

Fastigatocythere sp. Guha; 1976, ?Bathonian, India

F. accessa (Grekoff); in Guha, 1976, Upper Jurassic, India

Lophocythere (Fastigatocythere) aff. juglandica (Jones) in Rohr, 1976; Bathonian, southern France

**F. malzi* (Basha, 1980); Bathonian, Jordan and Egypt (Ex *Glyptogatocythere*)

F. naftaliensis Rosenfeld and Raab, 1984; Neocomian, Israel

Fastigatocythere sp. Dèpêche, 1985; Middle Bathonian, France

F. bakeri (Basha) in Rosenfeld et al., 1987; Bathonian, Egypt

*F. oblonga (Dèpêche, Le Hindre, Manivit and Vaslet, 1987); Middle Callovian, Saudi Arabia (Ex Amicytheridea)

*F. dierallaensis (Basha, 1980) form A Dèpêche et al., 1987; Bajocian, Saudi Arabia (Ex Amicytheridea)

*F. dierallaensis (Basha, 1980) form B Dèpêche et al., 1987; Upper Callovian, Saudi Arabia (Ex Amicytheridea)

*F. dhrumaensis (Dèpêche, Le Hindre, Manivit and Vaslet, 1987); Bajocian, Saudi Arabia (= Glyptogatocythere magharaensis Rosenfeld and Gerry in Rosenfeld et al., 1987) (Ex Amicytheridea)

*F. triangula (sic) (Bate) in Dèpêche et al., 1987; Upper Callovian, Saudi Arabia (Ex Amicytheridea)

F. juglandica (Jones) Brand 1990; Upper Bathonian, north-west Germany

F. grossepunctata (Chapman) in Malz and Oertli, 1994; Lower Bajocian, Australia

F. subiehiensis (Basha, 1980); Bathonian, Jordan, Egypt and Saudi Arabia (Ex Zerqacythere)

F. huniensis (Basha, 1980, pl. 4, figs 12–14); Bathonian, Jordan (Ex Zerqacythere); herein given the new name *Fastigatocythere jordanica*. This is necessary because Basha gave both a *Glyptocythere* species and a Zerqacythere species the name *huniensis*. Since we have decided that both belong to *Fastigatocythere*, one must be given a new name.

F. magharaensis (Rosenfeld and Gerry in Rosenfeld et al., 1987); Bajocian, Egypt

Fastigatocythere sp. Khosla and Jakhar, 1994 (fig. 4, 6-8); Upper Bathonian-Callovian, Kutch, India

Novocythere Rossi de García, 1972

The genus *Novocythere* was described by Rossi de García (1972, p. 271, pl. 1, fig. 7), from the Aptian–Albian of well SC-1, southern Argentina, with *N. santacruciana* as type species. According to the original description, the genus is pyriform, postero-dorsally upturned, strongly convex in dorsal view and ornamented by concentric puncta. Marginal denticles are present and the hinge is entomodont. The vestibulum is small and there are nearly 25 marginal pore canals anteriorly.

The same author (1977, p. 117, pl. 1) re-illustrated the genus using SEM and pointed out some further aspects of the morphology and age of *Novocythere*. At the same time, she differentiated it from *Majungaella* Grekoff and *Tickalaracythere* Krömmelbein on the basis of its lack of an eye tubercle and presence of an anterior vestibulum. However, her illustrations show that the type material has a low elongate ocular swelling which we interpret as an eye tubercle. With reference to the vestibula, no mention is made of this feature in the type description of *Majungaella* and, ironically, *Majungaella australis* Rossi de García and Proserpio, 1980 clearly shows a narrow anterior vestibulum. In the absence of any morphological criteria to separate this monospecific genus from *Majungaella*, we subsume it herein as a junior synonym.

Amicytheridea Bate, 1975

This genus, from the Middle Callovian of Tanzania, East Africa, was erected by Bate (1975) with *Procytheridea ihopyensis* Grekoff, 1963 as type species. *A. triangulata* Bate = *Procytheridea*? 3330 Grekoff, 1963, also from the Middle Callovian of East Africa, was also designated.

As diagnosed by Bate (1975, p. 91), *Amicytheridea* has a robust carapace, triangular in lateral outline and convex in dorsal view, with dorso-lateral ribs in an inverted chevron. The left valve is larger than the right. The eye tubercle and oblique post-ocular sulcus are clearly marked. The hinge is lobodont (with antero-median element loculate in the right valve). The anterior marginal pore canals number approximately 14.

Although he claimed that the hinge of *Amicytheridea* is lobodont, it can be seen (Bate 1975, p. 193, fig. 11 a–c) to be also entomodont. In fact, the difference between the two hinge types is only a matter of degree; in the lophodont hinge, the denticles on the antero-median element of the left valve are more distally expanded than in an entomodont hinge. We would not regard this as a generic character. In our opinion, *Amicytheridea* is synonymous with *Fastigatocythere* Wienholz, mainly because of its subtriangular shape, dorso-lateral inverted chevron ornament, ventro-lateral ribs parallel to the ventral margin, and clear eye tubercle and post-ocular sulcus. The antennal scar, however, is situated antero-centrally.

The emended diagnosis of *Fastigatocythere* (see above) includes *Amicytheridea* whose species are transferred and listed thereunder.

Tickalaracythere Krönmelbein, 1975

The genus *Tickalaracythere* was defined by Krömmelbein (1975) with two species, *T. ticka* (the type) and *T. scheibnerovae*, both from the Albian–Cenomanian of the Great Artesian Basin, Queensland, Australia. It has also been cited but not illustrated from the Campanian–Maastrichtian of the Sergipe Basin, eastern Brazil (Krömmelbein 1976, p. 546).

Krömmelbein (1975) erected this genus to separate from *Majungaella* some Upper Cretaceous species with robust and trapezoid-pyriform carapaces, which were postero-dorsally upturned, strongly convex in dorsal view, ornamented by a concentric pattern of punctations, with eye tubercle, shallow post-ocular sulcus and marginal denticles Their hinges are entomodont, anterior pore canals range in number from 24 to 28, and an anterior vestibulum is present in males. We believe these characters, in the context of the total range of characters within the plexus of *Majungaella* and *Tickalaracythere*, to be specific and not generic. Consequently, we regard *Tickalaracythere* as a junior synonym of *Majungaella* and have emended the generic diagnosis of the latter accordingly (see also Whatley *et al.* 1995a). Species previously assigned to *Tickalaracythere* are accordingly transferred, and listed under *Majungaella* (see above).

Glyptogatocythere Basha, 1980

The genus *Glyptogatocythere* was erected by Basha (1980, p. 241) with *G. malzi*, from the Bathonian of Jordan, as type species. Rosenfeld and Gerry *in* Rosenfeld *et al.* (1987, p. 260) described a second species, *G. magharaensis*, from the Bajocian of Egypt. As diagnosed, *Glyptogatocythere* Basha is subtriangular, ovate, centrally inflated in a triangular form; it is ornamented by subtriangular ribs in an inverted chevron with marked eye tubercle and oblique post-ocular sulcus. The left valve is larger than the right. The hinge is entomodont.

According to the type description and illustrations of *Glyptogatocythere*, we consider it to be synonymous with *Fastigatocythere* Wienholz, and its species are transferred.

Zerqacythere Basha, 1980

Basha (1980, p. 251) first described the genus with Z. subiehiensis as type species and with another new species, Z. huniensis; both came from the Bathonian of Jordan.

As diagnosed, this genus has a subtriangular carapace with a surface ornamented by sub-triangular ribs, in an inverted chevron, which overreach the dorsal margin and develop into complicated reticulation supported by two to three prominent, raised tubercles; the eye tubercle is prominent and there is a pronounced oblique post-ocular sulcus. The hinge, while allegedly lobobont, is clearly entomodont.

We consider that Zerqacythere is merely Fastigatocythere in which the ribs are broken up centrally into coarse reticulation creating prominent tubercles. We have, therefore, placed the two species of Zerqacythere within Fastigatocythere and consider the genus as a junior synonym. The emended diagnosis of Fastigatocythere Wienholz (see above) includes Zerqacythere, whose species are listed thereunder.

Dromacythere Ware and Whatley, 1980

This genus was separated by Ware and Whatley (1980) from its apparent closest relative, *Fastigatocythere* Weinholz, 1967. Named for its 'humped' dorsal margin, *Dromacythere* differs from *Fastigatocythere* and from other progonocytherids in its small size (0.41–0.48 mm adult length), exceptionally strongly developed entomodont hinge and the very strongly developed eye tubercle. *Arkellicythere* Ware and Whatley, 1980 is also small but has many more radial pore canals (18–22 anteriorly as opposed to eight anteriorly in *Dromacythere*). It was originally thought to be a progonocytherid but re-examination of its hinge has shown it to be antimerodont and the genus is, thereby, excluded from the family. It is possibly a protocytherid.

Dromacythere sagitta Ware and Whatley, 1980 (Text-fig. 1E–H) is the type and only known species of the genus, which does not seem to be particularly close to the other genera in the complex we have considered here. The following generic diagnosis is after Ware and Whatley, 1980. Small, subquadrate to globose, dimorphic, ornamented, progonocytherid, dorsally umbonate, with an eye tubercle and prominent post-ocular sinus. Radial pore canals few, straight, widely spaced. Hinge strongly entomodont, muscle scars type A (Bate 1963). Monotypic.

Strictocythere Sheppard in Brand, 1990

The genus *Strictocythere* was introduced by Sheppard (1981, p. 59) in her unpublished doctoral thesis to accommodate a group of species previously assigned to *Progonocythere*. Brand (1990, p. 207) used this name under the authorship of 'Sheppard *in* Brand'. Brand differentiated two subspecies from the type species *Progonocythere polonica*, *S. polonica polonica* (Blaszyk) and *S. polonica recta* Brand, both of them from the Upper Bathonian of north-west Germany (Brand 1990, pl. 13, figs 8–15 and figs 16–21 respectively). Malz and Oertli (1994, pl. 1, figs 4–5) described '*Strictocythere prolongata*' (nom. nov. pro *Loxoconcha elongata* Chapman, 1904) from the Lower Bajocian of Australia.

As diagnosed by Sheppard (1981) and emended by Brand (1990), *Strictocythere* is elongate-oval in shape, with anterior and posterior compressed margins, well rounded anterior margin and rounded triangular posterior margin with a short caudal process. The ventro-lateral border of valves slightly overhangs the ventral margin; the ornament is pitted and the hinge is entomodont.

We consider that *Strictocythere* is merely *Progonocythere* with elongate-oval lateral outline. Our emended diagnosis of *Progonocythere* incorporates the species of *Strictocythere* Sheppard *in* Brand and the genus is, thereby, subsumed.

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